VOLUME LX NUMBER 5

THE
BOTANICAL GAZETTE

*NOVEMBER 1915*

# OENOTHERA GIGAS NANELLA, A MENDELIAN MUTANT

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In a recent book GATES has studied the significance of the experiments made with species of *Oenothera* as proofs for the general theory of mutation, and has given an exhaustive and critical review of the facts in this rapidly increasing field of research.[1] He has laid special stress upon the results of crosses, which show the great diversity of these phenomena when studied in some wild plants, as contrasted with the now prevailing doctrine of Mendelism; for among the mutants of *Oenothera* instances of Mendelism are rare. The first known example is that afforded by *O. brevistylis*, which follows the law of MENDEL as a recessive in all its crosses with the parent species, with other mutants, and with other species of the same group.[2] But, unfortunately, the production of this form by means of mutation from *O. Lamarckiana* is so rare that it has not, as yet, been repeated under experimental control. Another instance is *O. rubricalyx*, discovered and studied by GATES (*op. cit.*, p. 103), which behaves as a dominant in its crosses with *O. Lamarckiana*.

In this article I hope to show that the dwarf character, which in so many instances complies with the formulae of MENDEL, but which behaves in a different way in crosses of the derivatives of *O. Lamarckiana*, may, at least in one instance in this group, follow that law as exactly as in any other pure Mendelian case. This

[1] GATES, R. R., The mutation factor in evolution. London. 1915.

[2] DEVRIES, HUGO, Die Mutations-Theorie. 1:223; 2:151–179, 429.

instance, therefore, affords a means for the experimental study of the origin of such a form by mutation. The main result of this study is the proof of the occurrence of mutant Mendelian hybrids besides the pure dwarfs.

In my book on the mutation theory I have pointed out that the origin of *O. brevistylis* from *O. Lamarckiana* may have been induced by the mutation of a single sexual cell. If this combined in fertilization with a normal gamete, a hybrid would be produced which would not be distinct from the parent species in its external features. This hybrid would then, in its self-fertilized seeds, follow the law of MENDEL and produce, besides constant *Lamarckiana* plants, partly hybrids of the same type and partly specimens of the type of *O. brevistylis*. From this origin and the subsequent free intercrossing in the field, the yearly appearance of *O. brevistylis* would receive a sufficient explanation (DEVRIES, *op. cit.*, p. 506).

If the process of mutation into this type were more often repeated, it should be possible to discover the original hybrids. They would, it is true, not be discernible from their normal sisters by external marks, but would yield, after artificial self-fertilization, about 25 per cent of *brevistylis*. And since mutants are produced ordinarily in a proportion of 1–2 per cent or less, the difference would be large enough to be noticed. Until now, however, such cases have not been observed.

I have, therefore, been looking for another example in which a Mendelian behavior of the mutants might be associated with a normal coefficient of mutation from the parent species. Such cases would betray themselves by exceptionally high coefficients in single parent plants. Instances of such individual deviations are very rare, partly on account of the necessarily limited number of mother plants from which the seeds of our cultures are taken. But SCHOUTEN[3] has observed that *Oenothera gigas*, which ordinarily produces 1–2 per cent dwarfs, may be seen to throw them off in as large a number as 15 per cent. The same phenomenon has been described by GATES (*op. cit.*, p. 137), who counted 9 per cent and 11 per cent of dwarfs among the offspring of two self-fertilized plants of *O. gigas*.

[3] SCHOUTEN, A. R., Mutabiliteit en Variabiliteit. 1908.

From time to time I have noticed the same deviating percentages in my own cultures. Thus, for instance, I fertilized in 1910 a specimen of *O. gigas* by its own pollen, and among 50 seedlings of its offspring 10 were dwarfs, pointing to a percentage of about 20 per cent.[4] Similar facts have since occurred more than once in my cultures.

SCHOUTEN and GATES have interpreted these figures as indicating a Mendelian proportion of dwarfs, and on this assumption the parent plant would have been a mutant hybrid in the same sense as explained above for *O. brevistylis*. Mutant hybrids would then occur in a race which produces dwarf mutants also, and the latter would then, of course, have to be considered as the products of the combination in fertilization of two sexual cells, both of which had mutated into *nanella*. The production of dwarfs from *O. gigas* would then follow the same process which is to be assumed for the origin of *O. gigas* itself from *O. Lamarckiana;* and the copulation of two similarly mutated cells would then more easily be accessible to experimental investigation.

In order to verify the exactness of this conception I have followed up the progeny of such a presumed mutant hybrid, and on the other hand have made crosses between *O. gigas* and *O. gigas nanella*. In both cases the truth of the assumption was easily ascertained.

Mutations of single gametes may be discovered by different means in other instances also, the production of potential *nanella* gametes by *O. Lamarckiana* being the most likely to be betrayed in this way.[5] I have observed such cases in crosses between *O. Lamarckiana* and *O. rubrinervis*. From these ordinarily two types arise in the first generation, one of which resembles the mother and the other the father. In my book on *Gruppenweise Artbildung* I have called them "*Lamarckiana*" and "*subrobusta*." Both types are usually constant after self-fertilization. But, from time to time, individuals appear which in their progeny produce an unexpected number of dwarfs. The following cases may be adduced.

[4] DEVRIES, HUGO, Gruppenweise Artbildung. p. 340. 1913.

[5] Besides the production of gametes for *gigas* by *O. Lamarckiana*, as shown by the occurrence of specimens of *semigigas* in self-fertilized strains of the parent species, or by the production of the Hero-type in crosses of *O. Lamarckiana* with allied species.

The *rubrinervis* strain for these experiments had arisen as a mutant from *O. Lamarckiana* in 1895, and its second generation was cultivated in 1905. No dwarfs were produced in the first generation after the crosses, and in the second only from single individuals, the remainder giving either no dwarfs at all or only about 1 per cent, by ordinary mutation.

TABLE I

EXCEPTIONAL PRODUCTION OF DWARFS BY SINGLE PLANTS OF *Oenothera subrobusta*

| Cross | Cross | 1 Gen. | 2 Gen. | Number of individuals | Percentage of nanella |
|---|---|---|---|---|---|
| Lamarckiana×rubrinervis.... | 1905 | 1913 | 1914 | 140 | 9 |
| rubrinervis×Lamarckiana..... | 1905 | 1907 | 1913 | 70 | 11 |
| rubrinervis×Lamarckiana..... | 1907 | 1913 | 1914 | 70 | 16 |

If we compare these figures with the results of the crosses between *O. rubrinervis* and *O. nanella* itself, as described in my *Gruppenweise Artbildung* (p. 215), we find a complete analogy, since these crosses give no dwarfs in the first generation, and in the second about 10–14 per cent from the self-fertilized specimens of *O. subrobusta*. It is evident, therefore, that the exceptionally high yield of dwarfs in these crosses of *O. Lamarckiana* and *O. rubrinervis* must be the product of latent mutations which occurred in some of the sexual cells of one of the parents. And since *O. Lamarckiana* is known to produce ordinarily 1–2 per cent dwarfs, while *O. rubrinervis* does not show signs of such a mutability, we may confidently assume that our figures indicate latent mutations of sexual cells of *O. Lamarckiana*.

BARTLETT[6] recently described a similar instance of an unexpectedly high mutability, and proposed for it the same explanation, on the assumption of a latent mutation of a sexual cell in a previous generation. This case is of the greatest interest since it relates to a pure species and not to the discovery of mutated gametes by means of crosses as in the experiments just described. The mutating species was *O. Reynoldsii* Bartlett, one of the forms of the old *O. biennis*. It produced in 1913 three marked types, one repeating the parental form, and the two others being dwarfs and called

[6] BARTLETT, H. H., Mutation en masse. Amer. Nat. 1915.

mut. *semialta* and mut. *debilis*. The latter is, on the average, about half as high as the former. This curious segregation repeated itself in the next generation in 1914, not from all the individuals, but from only one of the two whose offspring have been tried in this respect.

Similar proofs of latent mutations of sexual cells may evidently be expected to occur in other strains also and will have to be looked for in all cases of an unexpectedly high degree of mutability.

I will now return to my experiments on the production of dwarfs by *O. gigas*. In order to obtain specimens of *O. gigas* yielding a high percentage of dwarfs from their seeds, I sowed in 1911 seeds of my pure strain, cultivated the plants as biennials, and fertilized them in 1912 by their own pollen, in bags. They were vigorous plants of the fourth generation (*Gruppenweise Artbildung*, p.175), and yielded a large harvest of seed, which was sown in 1913, and served as a criterion, since no essential differences were to be seen on the plants themselves. Moreover, I used the seeds of some good biennial specimens of the previous or third generation. The ancestors of all these plants had been fertilized by myself in bags down from the mutant in 1896 which started the race. The harvest of 1912 and 1910, sown in 1913, gave the result as shown in table II.

TABLE II

A. Percentages of dwarfs among offspring of *O. gigas*

| Generation | Number of seed-bearer | Total of seedlings | Dwarfs | Percentage of dwarfs |
|---|---|---|---|---|
| 4th generation........ | 1 | 174 | 0 | 0.0 |
| " ........ | 2 | 176 | 1 | 0.6 |
| " ........ | 3 | 191 | 34 | 17.8 |
| " ........ | 4 | 154 | 1 | 0.6 |
| " ........ | 5 | 166 | 1 | 0.6 |
| 3rd generation........ | 6 | 164 | 0 | 0.0 |
| " ........ | 7 | 43 | 1 | 2.3 |
| " ........ | 8 | 52 | 0 | 0.0 |
| " ........ | 9 | 132 | 2 | 1.5 |
| " ........ | 10 | 130 | 0 | 0.0 |

From a second strain, derived from the same mutant and described in my *Gruppenweise Artbildung* (p. 175), I had in 1911–1912 nine biennial specimens which yielded a sufficient harvest.

Tried in the same way, they gave the percentages of dwarfs shown in table III.

TABLE III

B. DWARFS OF *O. gigas*

| Generation | Number of seed-bearer | Total of seedlings | Dwarfs | Percentage of dwarfs |
|---|---|---|---|---|
| 6th generation........ | 1 | 132 | 0 | 0.0 |
| " ........ | 2 | 165 | 0 | 0.0 |
| " ........ | 3 | 155 | 1 | 0.6 |
| " ........ | 4 | 161 | 0 | 0.0 |
| " ........ | 5 | 159 | 25 | 15.7 |
| " ........ | 6 | 76 | 0 | 0.0 |
| " ........ | 7 | 151 | 0 | 0.0 |
| " ........ | 8 | 130 | 0 | 0.0 |
| " ........ | 9 | 124 | 19 | 15.0 |

All in all, 19 specimens were studied. Among them three gave a percentage of 15–15.7–17.8, but the others gave only 1–2 per cent or no dwarfs at all. The dwarfs produced by this latter group were evidently due to ordinary mutability, but the figures for the former group differed too widely from these to be looked at in the same way. I consider them to be due to Mendelian segregation, and assume that the fact that they fall short of the expected 25 per cent is due to the difficulties of cultivation and to a less viability of the dwarfs as compared with the normal specimens.[7] I chose no. 3 of the first group (17.8 per cent dwarfs) for continuing the experiment.

If the segregation in this second generation followed the law of MENDEL, then among the plants of normal stature one-third must be constant in their progeny and the remainder must split up according to the same law. I succeeded in having a dozen of plants flower and ripen their seeds as annuals, fertilized them purely, and sowed the harvest in the spring of 1914. The result is given in table IV.

Three of the individuals yielded no more dwarfs than in ordinary mutation, and the seven others showed figures which approach the Mendelian law as nearly as might be expected. If we combine these figures with the 17.8 per cent of dwarfs of the former generation, we find for this about 18 per cent dwarfs, 57 per cent hybrids

[7] See GATES, *op. cit.*, p. 89.

of high stature, and 25 per cent normal high specimens. This may be considered as sufficient proof that the splitting took place after the law of MENDEL.

TABLE IV

C. DWARFS AMONG THE OFFSPRING OF *O. gigas* (A, no. 3)

| Number of seed-bearer | Total of seedlings | Dwarfs | Percentage of dwarfs |
|---|---|---|---|
| 1........... | 242 | 1 | 0.5 |
| 2........... | 276 | 0 | 0.0 |
| 3........... | 177 | 1 | 0.5 |
| 4........... | 237 | 39 | 16.0 |
| 5........... | 238 | 52 | 22.0 |
| 6........... | 236 | 50 | 21.0 |
| 7........... | 196 | 42 | 21.0 |
| 8........... | 81 | 25 | 31.0 |
| 9........... | 269 | 59 | 22.0 |
| 10........... | 265 | 57 | 21.0 |

The dwarfs were counted in June and July, and the degree of development at this time corresponded with the photographs given in my *Gruppenweise Artbildung*, p. 316, *figs. 115* and *116*. At this period they are clearly distinct from the normal specimens and so there was no difficulty in counting them. In some specimens of *O. gigas* mut. *nanella* the number of chromosomes has been determined and was found to be the same as in *O. gigas* itself (28), as was to be expected. Partly on account of this fact, partly in consequence of the nearer relationship, the fecundations did not experience the difficulties which are connected with crosses between *O. gigas* and *O. Lamarckiana* mut. *nanella*. They succeeded fairly well and yielded, as we have seen, relatively large numbers of seeds.

The Mendelian behavior of the production of dwarfs by means of mutation from *O. gigas*, moreover, may be proved in another way. If the mutant hybrids of this form are fertilized by the pollen of *O. gigas nanella*, the expectation will, of course, be the production of 50 per cent of tall specimens and 50 per cent of dwarfs. But, on account of the smaller viability of the latter, we should have to be content with somewhat smaller numbers. In 1913, therefore, I crossed some specimens of apparently normal *O. gigas* with the pollen of a constant race of *O. gigas nanella*, my culture being the third generation derived from a mutant of 1910 (*Gruppenweise Artbildung*, pp. 315–316). I was fortunate in choosing, among some normal plants, two mutant hybrids, and will give the constitution of their progeny, together with that of two normal individuals of *O. gigas*, in table V. The numbers of seedlings have been very small in this case, owing to the small degree of fertility of the pollen of *O. gigas nanella*.

TABLE V

DWARFS IN THE FIRST GENERATION OF *O. gigas*×*O. gigas nanella*

| Number of seed-bearer | Number of seedlings | Dwarfs | Percentage of dwarfs |
|---|---|---|---|
| 1 | 38 | 11 | 30 |
| 2 | 65 | 28 | 43 |
| 3 | 28 | 1 | 3 |
| 4 | 59 | 2 | |

The first two seed-bearers had evidently about one-half of their egg cells mutated into *nanella*, which by the fertilization with the pollen of dwarfs must, all of them, become *nanella* specimens. The two last-named plants, although externally not differing from the others, had only very few mutated sexual cells, and therefore produced only about 3 per cent of dwarfs.

TABLE VI

DWARFS IN THE SECOND GENERATION OF *O. gigas*×*O. gigas* MUT. *nanella*

| Seed-bearer | Total of seedlings | Dwarfs | Percentage of dwarfs |
|---|---|---|---|
| A. O. gigas nanella×O. gigas | | | |
| No. 1 | 291 | 45 | 15 |
| No. 2 | 69 | 12 | 17 |
| B. O. gigas×O. gigas nanella | | | |
| No. 1 | 60 | 16 | 27 |
| No. 2 | 310 | 73 | 24 |
| No. 3 | 304 | 62 | 20 |
| No. 4 | 74 | 14 | 19 |
| No. 5 | 283 | 46 | 16 |
| No. 6 | 210 | 30 | 14 |
| C. O. gigas mut. hybrid×O. gigas nanella | 326 | 52 | 16 |

The experiment showed at the same time that hybrids between *O. gigas* and *O. gigas nanella* have the features and the stature of the former type, and thereby justified the assumption made above in the explanation of the behavior of mutant hybrids.

I made the reciprocal cross in the same year, fertilizing some dwarfs of my race by the pollen of normal plants of *O. gigas*. The fecundation was a difficult one and I got only 38 seedlings, all of which developed into tall plants of the stature and character of *O. gigas* (1914).

In order to study the segregation of dwarfs in the next generation I fecundated a number of specimens of the three described groups of artificial hybrids and sowed their seed in 1915. On the basis of Mendel's law the expectation is, for all of them, 25 per cent dwarfs, or somewhat smaller numbers on account of the lesser viability of these dwarfs. The sowings of 1915, counted in May and June, gave the results shown in table VI.

These figures give sufficient proof that the crosses between *O. gigas* and its dwarfs follow the law of MENDEL.

**Summary**

1. *Oenothera gigas* produces dwarfs (about 1–2 per cent) and mutant hybrids of normal stature, which after self-fertilization give 15–18 per cent, theoretically 25 per cent, of dwarfs.

2. These mutant hybrids split up, after self-fertilization, according to the law of MENDEL, yielding about 18 per cent dwarfs, 25 per cent normal specimens of tall stature, and 57 per cent hybrids of the same type. The latter gave about 21 per cent of dwarfs among their progeny.

3. The mutant hybrids, fertilized by *O. gigas nanella*, yield 30–43 per cent, theoretically 50 per cent, of dwarfs.

4. In artificial crosses with *O. gigas* the dwarfs follow the law of MENDEL.

5. The production of dwarfs from *O. gigas* by means of mutation, therefore, is to be considered as requiring the copulation of two gametes, both of which are potentially mutated into dwarfs. The mutant hybrids must then be the result of the fertilization of a mutated gamete by a normal one. They are correspondingly less rare than the dwarfs themselves.

6. In combination with the fact that the dwarfs of *O. Lamarckiana* do not follow the law of MENDEL, either in their origin by mutation or in artificial crosses with the parent species, these conclusions reveal a new differential character between *O. gigas* and its parent species.

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